VEGETATION AND PLANT COMMUNITIES
OF SOUTHERN CALIFORNIA DESERTS
-- A FUNCTIONAL VIEW

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INTRODUCTION

In light of the comments by other participants in this symposium, the title I have chosen probably appears to have been selected for purposes of political expediency. We have heard some rather strong declarations about the non-existence of plant communities. Those holding such views seem to be perfectly happy, however, in talking about vegetation. Others have dis-cussed plant communities in great detail without any qualms of conscience. Dr. Ted Hanes and Dr. Richard Vogl have seemed to suggest that perhaps the recognition of plant communities is borne out of practical necessity more than objective reality. At the risk of appearing too conciliatory, I would like to argue in favor of both vegetation and plant communities as separate but closely related concepts, both having validity for interpreting the plant cover of the earth.

With regard to vegetation, I view it as something that is best defined in terms of structure and function with an emphasis on function, especially as increasing knowledge allows us to tie structure and function together at all the various levels of biological organization. I must confess that my prejudice in this matter stems back to my former mentor, Pierre Dansereau, who over the years has been greatly concerned with vegetation structure and classification (Dansereau 1951, 1966). On the other hand, plant communities, I believe, are best defined on the basis of floristic considerations, i.e., taxonomic composition. The distinction between the vegetation and floristic approach is rather easily drawn, even though beginning students are often confused by the matter since plants are the basic concern in both instances. The two contrasting points of view are admirably represented in the volume entitled "The Vegetation and Flora of the Sonoran Desert" by F. Shreve (responsible for the vegetation) and I. Wiggins (responsible for the flora) (Shreve and Wiggins 1964). I teach a course in which I insist that students be able to distinguish between the two philosophies or points of view repre-sented in this title. On a final exam, one particularly clever student responded to the challenge of making this distinction by observing: "To a person interested in flora, a rose is a Rosa is a Rosaceae. To a person interested in vegetation, a rose is a rose is a shrub." I felt the answer deserved an A grade.

I would like to extend this bit of wisdom a step further to separate the concepts of plant communities and vegetation. To a person interested in com-munities a native rose in southern California is merely an occasional member of the riparian woodland community. To a plant ecologist devoted to the idea of structure and function of vegetation, a rose would more likely be regarded as a small shrub with compound leaves, prickly stems and the C-3 pathway for

photosynthesis. The point needing emphasis here is that the concepts of plant communities and vegetation are not necessarily hierarchical as might be suggested by the customary practice of constructing classification systems in such a way that plant communities are listed as subdivisions of larger vegetational zones, e.g., Munz and Keck (1949 & 1950). We must recognize that fundamentally different criteria are usually employed in defining vegetation types than are used in characterizing plant communities.

The drastic shifts in criteria that occur in passing from communities to vegetation thus present problems for logical classification schemes. It should become readily apparent that both criterion sets could be further refined or grouped to provide smaller or larger units that could then be arranged in an hierarchical order. This sort of rationale has been rigorously followed by European workers of the Braun-Blanquet school of phytosociology (Mueller-Dombois and Ellenberg 1974). The basic units upon which their classificational system depends are formally defined plant associations characterized on the basis of plant taxa. The associations are grouped into alliances and sometimes the alliances into orders and the orders into classes. Associations, the fundamental unit, are defined as plant communities of definite floristic composition and uniform physiognomy occurring in uniform habitat conditions. Thus the success or failure of the classification scheme is based on the objective reality of plant associations. This completely integrated approach has not been used to any great extent in North America, presumably because of difficulties encountered in identifying and agreeing upon what constitutes the associations. It must be noted, however, that the resistance to the general acceptance of this approach has not dissuaded numerous investigators from going ahead and describing communities along much the lines as those set forth for plant associations. The concept used by Munz and Keck (1949 & 1950) for describing the plant communities of California provides a prime example of this. Other investigators have interpreted the meaning of plant community much more loosely and have used the same terminology to describe assemblages of plants of vastly different scale.

Now what does all this have to do with the title of my subject? Through the years, a considerable body of heterogeneous literature has accumulated concerning the plant life of the North American deserts and what I hope to do is draw somewhat on this fund of knowledge for the purpose of this paper. I am not going to propose to try and solve the problem of the nature of plant communities with respect to flora and vegetation in the few pages allotted me but I will merely try and use some of the information and ideas that I have accumulated on the subject as it pertains specifically to the deserts of California.

SUBDIVISIONS OF THE CALIFORNIA DESERT

The desert region of California is generally considered to consist of two parts, popularly referred to on the daily weather report as the high and low deserts. More specifically, these desert areas are designated as the

Mojave (high desert) and the Colorado (low desert) (Fig. 1) (Shreve 1935; Jaeger 1965). Together they comprise about two-thirds of the total land area of the region that may be conveniently designated Southern California (Munz 1974). An additional segment of desert, or near desert, may also be recognized in the southwestern part of the Central Valley. All three areas are readily distinguished on the basis of physiographic, climatic and biotic features. The boundaries setting off the two principal deserts, the Mojave and the Colorado, are particularly sharp on the western and southwestern interface. Toward the east, the boundaries become less distinct and any line drawn to demarcate the southeastern boundary of the Mojave and the northeastern limit of the Colorado Desert can only be arbitrary. This appears to be the case regardless of whether one relies on physiographic, climatic or biotic criteria.

PHYSICAL FEATURES

Physiographically, the Mojave Desert lies at elevations generally above 600 meters (2,000'), at least in its southwestern extension. At the point of its first interface with the Colorado Desert to the east along the Little San Bernardino Mountains (in the vicinity of 29 Palms) it has an elevation of approximately 1,000 meters (3,300'). To the south, the elevation of the Colorado Desert decreases rapidly, falling to sea level at Indio and well below sea level still farther south. This zone of rapid elevation change constitutes a clear boundary which corresponds to changes in the climate and biota. The southwestern boundary of the Mojave extends well beyond that of the Colorado and is sharply marked by the spectacular San Andreas and Garlock Faults which come together to form a "V" shaped corner at the intersection of their associated mountain ranges, the San Gabriels on the south and the Tehachapis on the west (Sharp 1972). The San Andreas Fault continues on into the Central Valley where its association with the South Coast Ranges produces a rain shadow that gives rise to a desert-like area in the western part of the Central Valley itself. Toward the north, the Mojave Desert boundary remains rather distinct.

In the extreme northern portion of the southern California desert region is found the anomalous Death Valley, which plunges to a depth of −86 meters (−282') below sea level to become the lowest point in North America and which should perhaps be considered as a separate entity because of its many unique features. For our purposes, however, I will merely consider it as a feature marking the northern reaches where the Mojave interfaces with the Great Basin Desert. To the northeast, the Mojave extends out of California, through Nevada, to the southwestern corner of Utah. This boundary is marked to the north by a rather abrupt rise in elevation to the comparatively higher plateaus and valleys of the Great Basin. The eastern boundary is at first distinct on the north but becomes blurred as it merges with the Sonoran Desert to the south. Here there is little in the way of physiographic features to assist in drawing a boundary line to designate the beginning of the Sonoran Desert. The Colorado Desert of California is therefore very
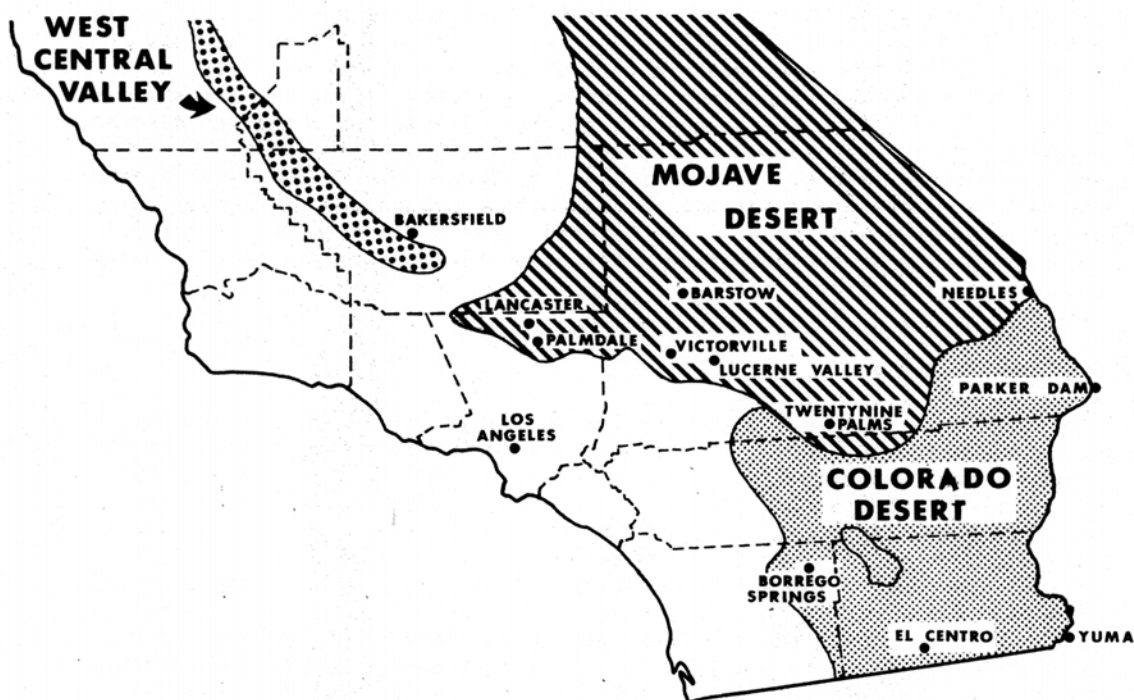
Figure 1. Deserts of southern California. The towns located on the map in the desert areas are those for which climatic data are given in Table 1.

closely related to the Sonoran Desert of Arizona, Mexico and Baja California and physiographically should be considered as a representative division of this greater unit (Shreve 1951).

CLIMATE

The climatic differences between the two principal deserts can be readily seen from temperature and precipitation data (Table 1). The means of July and January temperatures for the Mojave are generally around 10 F lower than for the Colorado. The proportion of the total annual precipitation falling in the summer is also noticeably less in the Mojave but shows a marked increase toward the fuzzy boundary on the east. The sparseness of summer rain in the southwestern corner of the high desert must be due to the shielding effect of the San Bernardino and San Gabriel Mountains which intercept and block summer storms that characteristically follow a storm track coming from the southeast. Storms moving in from the west and southwest during the summer period are practically non-existent. The southwestern Central Valley has essentially the same climatic regime as the southwestern Mojave, cf. the reading for Bakersfield (Table 1). The proportional increase in summer rain in the direction of the eastern Mojave tends to emphasize the problem of drawing a boundary line between the two deserts at their southeastern-northeastern margins, cf. Needles and Parker Dam. Death Valley again appears anomalous. The climatic data for the stations in the Colorado Desert support the contention that it is very similar to other parts of the Soronan Desert, e.g., 41% of the precipitation in Phoenix, Arizona, an unquestionably Sonoran location, comes during the four summer months and the mean July temperature is 90 F while that for January is 50 F.

FLORA

The biotic differences between the high and low deserts have been long recognized. The discussion here will be restricted to considerations of the plant life. Two of the deans of desert botany, Philip Munz (1935) and Edmund C. Jeager (1941), have commented in detail on differences in the flora. In 1935, Munz calculated that only 45% of the species found in the California deserts were common to both desert areas. Parish (1930) was impressed in the same manner and said that of the 545 species which he knew to be in the Mojave Desert, 263 (48%) did not extend into the Colorado Desert. This outstanding feature of the Mojave flora depends to a large extent on two factors: 1) the large number of Great Basin species that enter the Mojave from the north but do not extend to the low desert farther south, e.g., Artemisia spinescens and Atriplex confertifolia (Beatley 1975, Billings 1951); and 2) the large number of endemics, particularly from the southwest corner, Death Valley region and isolated mountain ranges to the east. Endemic status is represented mostly by species that presumably have a recent evolutionary origin, i.e., neoendemics as opposed to paleoendemics that attain endemic status through the selective extinction of what was once more widespread populations.

Table 1. Climatic summary of selected stations from California deserts and near vicinities (Bailey 1966, Felton 1965).

Location	Annual ppt. in.	Summer* ppt. in.	% ppt. in summer	Mean July Temp. °F.	Mean Jan Temp. °F.
Southwestern Central Valley					
Bakersfield	6.00	0.21	3.0	83.4	47.0
Mojave Desert					
Backus Ranch	7.15	0.47	6.6	82.7	42.6
Lancaster	5.2	0.01	0.2	81.8	41.3
Palmdale	9.12	0.56	6.1	81.1	43.6
Victorville	5.99	0.50	8.3	77.6	41.7
Barstow	4.25	0.69	16.2	84.0	45.7
Lucerne Valley	4.11	0.81	20.0	81.9	44.2
Twenty-nine Palms	4.20	1.60	38.1	88.3	48.1
Needles	4.63	1.48	32.0	94.2	51.2
Death Valley	1.66	0.33	20.0	101.7	51.5
Colorado Desert					
Parker Dam	5.36	1.79	33.4	95.3	52.0
Yuma	3.40	1.30	38.2	94.6	55.3
El Centro	2.81	0.80	28.5	92.2	53.4
Borrego Springs	3.99	1.73	43.4	89.1	50.4
Indio	3.20	0.65	20.3	93.0	53.7

* Summer precipitation is taken at the total for the months of June, July, August and September.

A brief survey of plant distributions as given in Jaeger's "Desert Wildflowers" (1941) and Munz's new "A Flora of Southern California" (1974), seems to confirm the suspicion that annual species from the evolutionarily dynamic families, Polemoniaceae, Hydrophyllaceae, Onagraceae and Asteraceae, contribute heavily to this distinctive endemic characteristic. Twisselman (1967) lists Gilia cana, Phacelia nashiana, Camissonia kernensis and Hemizonia arida from the respective families as having distributions restricted to eastern Kern County which in large part is equivalent to the southwestern Mojave. He reports that 25 species from Kern County are endemic to the Mojave Desert. The endemism of the Death Valley region is well known and includes unique genera such as Gilmania and Oxystylis, as well as numerous species, e.g. Enceliopsis covillei, Eriogonum rixfordii and Boerhaavia annulata. The mountain slopes of the eastern Mojave harbor species, such as Agave utahensis, Forsellesia pungens and Camissonia walkeri, not found in other parts of California.

The degree of endemism in the Colorado Desert is much lower than for the Mojave (Munz 1935), but is characterized by an unusually high number of what have been characterized as relictual species (Stebbins and Major 1965). Washingtonia filifera, Fouquieria splendens and Olneya tesota may be considered as belonging to this group, even though their distributions extend beyond the Colorado Desert into other parts of the Sonoran.

The boundary between the two deserts might be considered as being marked by the northern extension of a fairly large number of conspicuous Colorado (Sonoran) Desert small trees and shrubs. Among the most obvious (Hastings et al. 1972) are:

Beloperone californica	Fouquieria splendens
Cercidium floridum	Hyptis emoryi
Condalia globosa	Olneya tesota
Dalea emoryi	Opuntia bigelovii
Dalea spinosa	Simmondsia chinensis
Ephedra trifurca	Trixis californica

The northern limits in eastern California of these species coincides in a general way with a shift to Mojave taxa. The zone of contact is a complex mosaic, however, and enclaves of either of the two intermingling floras may extend well beyond any single line that might be drawn in an effort to separate them.

The flora of the southwestern Central Valley area is largely made up of coastal taxa along with many introduced weeds. Of special note, however, are two desert species, mesquite (Prosopis juliflora) and common saltbush (Atriplex polycarpa), which give a desert aspect to the landscape. In addition, the occurrence of a few plants of Larrea tridentata growing naturally in the Valley attests to the true desert character of the area (Twisselman 1967). Desert alkali sink species reminiscent of playas in the Mojave are also present in the bottom of closed drainage basins. The vegetational character of this region is presently undergoing rapid and drastic change.

Vast acreages of new land are being put under cultivation each year in response to the newly available irrigation water supplied by the recently completed westside canal.

PLANT COMMUNITIES

According to Axelrod (in Munz and Keck 1959), the flora of the Mojave Desert is derived from the Arcto-Tertiary geoflora while that of the Colorado Desert is thought to stem mostly from Madro-Tertiary elements. Stebbins and Major (1965) offer an alternative hypothesis for the latter and suggest its derivation from a more ancient xeric, or semi-xeric, element that existed in widely distributed arid habitats prior to the development of the Madro-Tertiary geoflora. This theme is further elaborated by Johnson (1968). He suggests that long persistent sand dune and saline habitats along the coast may have served as an important source of plant colonizers for the interior as increasing aridity brought about the development and expansion of deserts in western North America. Whatever the situation, various communities have differentiated with the available flora serving as the basic building blocks. The kinds of communities that contemporary botanists recognize are commonly described on the basis of taxonomic composition, structure, and/or habitat (Table 2). The problem of community nomenclature is rather overwhelming. However, Dr. Thorne has attacked this problem nobly in his paper in this volume. The selected classification schemes presented in Table 2 show that some names are based on taxonomic units, e.g., shadscale shrub, some on structural units, e.g., stem-succulent scrub, and still others on properties of the physical habitat, i.e., alkali-sink and desert wash.

It must be recognized that different purposes have stimulated the construction of the different classification systems represented in the table. Munz and Keck (1959) specifically state that their purpose for characterizing the plant communities of California was to provide an extra aid in the use of their flora for purposes of plant identification. Küchler (1964), with the orientation of a geographer, has the compulsion to map the distribution of all the vegetation in the world, and so for him a matter of scale becomes all important. On a 40" x 60" map of the United States, how do you designate small units, such as alkali sink scrub and palm oases, regardless of how objective their reality seems when standing beside them on the ground? Küchler is, however, consistent with his generic nomenclature in designating his "vegetation types". Jaeger and Smith (1966), Thorne (1976) and Knapp (1965) are obviously more interested in using the community concept as a means for organizing biological information and perhaps even to promote the idea that the resulting combinations recognized have biological significance giving enlightenment on matters of evolution and adaptation. The special kinds of communities that are unique to each of the last three authors are informative in suggesting differences in the ways they look at the plant world. Jaeger and Smith are particularly notorious at mixing biotic and habitat criteria in their nomenclature (e.g., sagebrush scrub vs. desert wash). This is rather bothersome to those of us who feel that plant communities should be given names in accordance with plant features

Table 2. "Plant Communities" of the California deserts compiled from the works of Munz and Keck 1949 and 1950, Küchler 1964, Jaeger and Smith 1966, Thorne 1976, and Knapp 1965.

Munz and Keck	Küchler	Jaeger and Smith	Thorne	Knapp
Sagebrush scrub	Great Basin sagebrush	Sagebrush scrub	Great Basin sagebrush scrub	Sagebrush desert
Shadscale scrub	Saltbush-greasewood	Shadscale scrub	Shadscale scrub	Shadscale desert
—	—	—	Blackbush scrub	Blackbush desert
Alkali sink	—	Alkali sink	Alkali sink scrub	Atriplex, alkali soil desert vegetation
—	—	—	Alkali meadow	Saltgrass desert meadow
—	—	—	—	Iodine bush alkali soil desert vegetation
Joshua tree woodland	—	Joshua tree woodland	Joshuatree woodland	Joshua tree desert
Pinyon-juniper woodland	Juniper-pinyon	Pinyon-juniper woodland	Pinyon-juniper woodland	Pinyon-juniper woodland
Creosote bush scrub	Creosote bush	Creosote bush Low desert scrub	Creosote bush scrub	Microphyllous Creosote bush desert
—	Creosote bush bur sage	—	—	—

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Table 2. (continued)

Munz and Keck	Küchler	Jaeger and Smith	Thorne	Knapp
—	Paloverde - cactus shrub	Desert wash	Desert riparian woodland	Paloverde arroyo scrub
—	—	—	Desert microphyll woodland	Mesquite scrub
—	—	—	Desert oasis woodland	Palm oasis
—	—	—	Semi-succulent scrub	
—	—	—	Stem-succulent scrub	
—	—	Desert sand dunes	Desert dune sand plants	
—	—	*Colorado River bottom	*Desert rock plant (rupicoles)	*Winter annual vegetation
		*Desert canal	*Non-basic rock plant	*Summer annual vegetation
		*Desert urban	*Basic rock plant	
		*Desert rural		

* Unique listings, i.e., those that do not seem to have counterparts in any of the other classification schemes.

rather than habitat properties. Their classification scheme is distinctive from another point of view, however, since they include some of the unique plant assemblages that have been brought about by the intervention of modern man (e.g., desert canal and desert urban). Thorne's classification is based on biotic factors, but of two different types, as he freely mixes structural and taxonomic categories in his community designations (e.g., shadscale scrub and stem-succulent scrub). Knapp's basic community units are based on the presence of certain taxa, except for his last two categories - summer and winter annuals - which appear as anomalous additions and represent a marked shift or extension of the criteria he must have used for defining his communities; without them, it might have been assumed that he regarded communities as units in the landscape having discrete spatial limits. The inclusion of winter and summer annuals communities adds a temporal component to his definition since they in all probability must simultaneously occupy the same space as the perennial community or communities in which they are immersed, even if for only a very short period of time. We will come back to this point again later.

The problem of "lumpers" and "splitters" so renowned in taxonomy is in evidence in community nomenclature also, cf. Munz and Keck with Thorne (Table 2). In general, the communities (sagebrush, shadscale, blackbush, etc.) listed at the top of the table are only present or best developed in the high desert. Those appearing toward the bottom of the table, starting with creosote scrub, which is the most common community on both deserts, are more characteristic of the low desert. The additions by Jaeger and Smith, Knapp and Thorne to the much coarser treatments by Munz and Keck and Küchler are significant and tend to set in proper perspective certain important realities about community organization among desert plants. The earlier, shorter treatments have tended to slight the deserts, perhaps because they are less well-known than some other parts of the state. The more local one's interest in native plants, the greater the service rendered by the splitters. Local listings of species are of great value to professional researchers as well as amature field biologists. The various authors cited above provide lists of species that they recognize as being most characteristic of the communities they describe. I refer you to Dr. Thorne's paper in this volume as an excellent source for this type of information.

It must be understood that the community types summarized in Table 2 have not been defined in terms of association tables a la Braun-Blanquet, or by any other semi-objective means. The authors responsible for them appear to have arrived at their decisions on the basis of intuition born from extensive field experience. The objective characterization of the community types in California is a task still awaiting a capable devotee.

In keeping with this same intuitive approach, I would suggest that five additional communities be listed with those already proposed:

1) Joshua Tree Grassland. In the eastern Mojave in the vicinity of the New York Mountains, there are large areas where species of Bouteloua and Hilaria dominate the vegetation. Scattered Joshua trees throughout the area give rise to the suggested designation. Vegetation with this

same general association of species is more extensively developed farther east in Arizona.

2) Hopsage Scrub. In the Panamint Mountains near Death Valley, there are extensive stands dominated by Grayia spinosa which should be designated as a community. This also is more extensively represented to the east as indicated by Beatley's studies in Nevada (Beatley 1974a).

3) Cheesebush Scrub. The drainage channels or washes of the Mojave Desert have a different mix of species than do those of the Colorado Desert to the south. The "desert wash" designations of the authors cited above seem to refer only to the latter. I propose recognition of a Mojave "cheesebush scrub", characterized by Hymenoclea salsola, Atriplex polycarpa, Chrysothamnus paniculatus and Acacia greggii.

4) Allscale Scrub. Broad rolling expanses of Atriplex spinifera and Atriplex polycarpa occur in western San Bernardino County and the desert parts of Kern County. This general aspect does not fit the usual community designation for these species which links them with alkali sinks (Table 2). Indeed, the extension of this particular assemblage into the southwestern part of the Central Valley forms the basis for arguing the presence of desert in the Central Valley in the first place.

5) Desert Holly Scrub. Desert holly (Atriplex hymenelytra) dominates large areas in Death Valley that are not particularly alkaline or saline (Hunt 1966). A community designation "Desert holly scrub" seems appropriate.

A very different approach to the consideration of plant communities is represented by the work of McHargue (1973) for the Coachella Valley of the Colorado Desert. He adheres to the continuum point of view which contests the existence of discrete communities. He discusses the distribution of perennial taxa along altitudinal and soil-textural gradients. He voices some disappointment in not finding good agreement between his indirect ordination of the important perennial species and a direct ordination of habitat characteristics. He notes this lack of agreement may in part be due to distributional characteristics which are especially pronounced in desert communities. Perennial species often range over a wide spectrum of soil conditions only to stop abruptly and conspicuously at a particular line. Sometimes the line represents a change in soil properties and other times it apparently does not. Such discontinuities in space, though common in many climatic zones, are particularly pronounced in stressful environments such as deserts. Desert annuals seem to have more selective habitat requirements than perennials, as we shall see below, and if McHargue could have included them in his analysis he may have found a continuous intergradation of species distributions which the methodology used in his approach is designed to show.

VEGETATION

Forrest Shreve (1942, 1951) was a champion of the belief that mixed floristic and structural criteria should not be used indiscriminately in making classification schemes of the earth's plant life. He outlined the following categories as representing different logical frameworks for studying desert plants: 1) taxonomic units (flora); 2) the patterns of association among the taxa (communities); and 3) the kinds of plants present (structural-functional types making up the vegetation).

Dynamics of Desert Vegetation. Justification for viewing desert vegetation on the basis of structure and function in addition to the traditional species distribution approach is supported by the fact that species and communities of species vary structurally and functionally in both time and space. This becomes important if we accept the proposition that a principal goal of biology is to gain an understanding of the relationship between structure and function at all levels of biological organization ranging from organelles up to and including whole communities. At the level of vegetation, it can be argued from a biophysical point of view that structural configuration sets limits on physiological alternatives. For example, leaf size has a definite causative relationship with leaf temperature and therefore an influence on a whole host of temperature sensitive metabolic events.

I should mention the use of the term "function" herein, although in agreement with the way it is used generally in biology, contrasts with the way it is frequently used in vegetation discussion. In such discussions, changes of structure in time, such as the seasonal dropping of leaves, is often considered as a functional characteristic (Dansereau 1951). Changes in time at the community level not only make community definitions difficult, but further complicate the effort of viewing them as functional units, except perhaps in terms of the somewhat metaphysical Clementsian association concept.

It is a popularly-held view that mature natural communities are at a state of development known as "climax" which conjures up what may be false visions of balance in nature. Mounting evidence suggests that the vegetation of our desert is not static at the present time nor has it been for any great periods of time in the past. This becomes clear from the work on ancient woodrat middens pioneered by Philip Wells (Wells and Jorgenson 1964, Wells and Berger 1967). Investigators working in this area have discovered that the compulsive habit of woodrats (Neotoma spp.) to gather and store the vegetation from surrounding terrain has persisted for centuries. Plant fragments stored in such caches have made it possible to reconstruct a vegetation history dating back thousands of years. One important conclusion from these studies is that much of the Mojave Desert now occupied by microphyllous scrub was covered with juniper-pinyon woodland as recently as 10,000 years ago.

A most interesting gap in the record of extant plants found in the C^{14}-dated rat middens older than 11,000 years is the seeming lack of creosote

bush (Larrea tridentata). This observation is particularly exciting to
Dr. Frank Vasek, myself and some of our students, since we have found
reason to believe that living creosote bushes, in some of the areas from
which junipers remains have been found, are very old, on the order of thou-
sands of years (Vasek, et al. 1975). This leads us in a wild burst of
imagination to the conclusion that some Larrea plants which are living
today may represent the initial first-generation establishment! The impli-
cations this may have in terms of origin, composition and stability of
desert plant communities are rather extreme. Great age may contribute to
community stability in terms of continuity in time, but in so doing repre-
sents a marked departure from the customary view that stability results
from a kind of reproductive balance in which a stable age distribution is
maintained.

The question of whether communities exist as more or less discrete
functional units in time and space cannot be answered satisfactorily on the
basis of species distribution and composition. Structural and probable
functional differences within species throughout their distributional range
pose problems to a functional community concept if the communities are
defined solely on the basis of taxonomic units. For example, Larrea triden-
tata, the most characteristic plant species of the southwest, is represented
in North America by three different chromosome races. The distribution is
reported generally to be 1) diploids in the Chihuahua Desert, 2) tetraploids
in the Sonoran Desert, and 3) hexaploids in the Mojave (Yang 1970). These
races, on the whole, represent different functional categories. Even where
they are mixed, they probably occupy contrasting microsites.

Experimentation on the salt tolerance of Atriplex nuttallii in the
Great Basin gives an indication of how great the range of functional types
may be within a species (Goodman 1973). Broad differences in salt tolerance
were found to exist between populations of this species over a rather short
spatial distance. These sorts of observations suggest the possibility that
sharp boundaries between plant communities may indeed represent rather abrupt
changes in the functioning of the whole community and that one ecotype of a
species may be filling one role in a given community while another ecotype
may fill quite a different role in an adjacent community. Such probabil-
ities present considerable difficulty for applying functional interpre-
tations to the overlapping bell-shaped species distribution curves that
appear so ubiquitously in the literature.

Species of the important genus Eriogonum provide further examples.
Cole (1967) studied photosynthetic characteristics of different populations
of several Eriogonum species and found that different species from the
same habitat were more similar than were the populations of the same species
from different habitats. This suggests that the forces operating to bring
about convergence in ecosystems may have just as much significance, and
in this case perhaps even more from a functional point of view, as do those
which caused the differentiation of the recognizable taxonomic units.

The existing structure of desert vegetation provides infinite opportunity for evaluating correlative patterns between dynamic biological and physical processes that have become established through time. To date, however, little experimental work has been done with plants in the determination of functional consequences of specific structural alternatives; consequently, we are somewhat limited in the extent to which we can proceed with analysis at the functional level. This limitation is not imposed because functional interpretations of morphological and anatomical modifications are lacking in the literature, since indeed they are legion, but because such interpretations are generally based on teleological rather than experimental confirmation (Maximov 1931, Johnson 1975). At present, it seems advisable to keep structural considerations separate from functional ones unless the correspondence between them has been clearly demonstrated.

STRUCTURE. Structural differentiation in the desert with respect to space and time is most obvious at the level of growth habit, or life form. The principal growth habits represented are woody plants, succulents, perennial herbs and annual herbs. Woody plants are comprised of small trees and shrubs. Small trees (Cercidium floridum, Olneya tesota, Dalea spinosa, Chilopsis linearis, Prosopis glandulosa) are restricted to, or are markedly more common in, the Colorado Desert than in the Mojave. They appear most conspicuously along drainage channels, and in the vicinity of the Chuckwalla and Chocolate Mountains they cover rather broad expanses in the enlarged Arroyo Seco and Wiley Wash areas. All trees contain a high proportion of their chlorophyll in or under the bark of their stems and with the exception of desert willow are either aphyllous or microphyllous.

Shrubs in both deserts are responsible for the major structural aspect of the vegetation found on extensive bajadas and lower mountain slopes. Even though the species may differ from place to place, their sameness in appearance has been described by some as monotonous, especially in the Mojave. Like the small trees, their shoots are mostly either aphyllous or microphyllous, with abundant chlorophyll in the younger bark tissue, even though the latter may be obscured by pigmentation or discoloration of the outer bark layers. The leaves, when present, are small in surface area, usually rather soft and thick, and may or may not be covered with a layer of hair. Sclerophyllous leaves, often said to be characteristic of arid land vegetation, are generally lacking; jojoba (Simmondsia chinensis) in the Colorado Desert is an exception.

Succulents are common and may be conveniently categorized as halophytes and non-halophytes. Succulent halophytes are characterized by succulent leaves and stems, the capacity for maintaining high salt concentrations in the vacuoles of living cells, and the occupancy of highly saline habitats. Plants belonging to this group (mostly the chenopods (Allenrolfea and

Suaeda) are found in closed drainage basins in the Colorado, Mojave and
Central Valley deserts where the soil is continually moist. In the non-
halophytes, two major types may be recognized: those with succulent stems
(Cactaceae) and those with succulent leaves (Agavaceae). Though both families
are represented on both deserts, the former is more prominent in the vege-
tation of the Colorado and the latter in the vegetation of the Mojave.
Further spatial patterns within these deserts may also be recognized but
this consideration will be reserved for later treatment of unique functions
which are closely associated with the succulent habit.

Perennial herbs, primarily grasses, make important contributions to the
vegetation in the southeastern Mojave. These also have important functional
implications which will be considered below. In other parts of the deserts,
the seasonal contribution of perennial herbs during periods of available
moisture is rather meager, in contrast to annual herbs which show distinct
differentiation into summer and winter components.

A recurring change of vegetation structure with respect to climate and
time is commonly observed in many woody and herbaceous plants. Two aspects
of the temporal component of structure are particularly impressive: 1) the
presence or absence of leaves on woody plants, and 2) the sudden appearance
of annuals when the appropriate environmental conditions are satisfied. The
deciduous habit is markedly seasonal in some species, e.g., mesquite (Prosopis)
and desert willow (Chilopsis) but is drought-triggered in others, such as
ocotillo (Fouquieria) and paloverde (Cercidium). Most shrub species may be
fitted into either of these categories although a few, such as Peucephyllum
shottii, are persistently evergreen.

Desert annuals grow in response to threshold levels of moisture and
form two distinct groups: 1) those which respond to summer rain and 2) those
which are triggered by fall and winter precipitation. The leaf anatomy of
these two groups differs in the way the chlorophyll is organized with re-
spect to the vascular tissue. This relationship provides an obvious start-
ing point for asking some basic questions about structural-functional
relationships.

FUNCTIONAL CONSIDERATIONS. Recently a most interesting relationship
has emerged regarding the correlation between the fundamental process of
photosynthesis and the structural organization of the tissue in which the
process takes place. Photosynthesis, which for many years was thought to
proceed in the same manner in all plants, is now known to proceed by at
least two alternative pathways. At the biochemical level, the difference
is represented by the first products of carbon dioxide fixation. From the
early 1950's to the mid 1960's, it was widely believed that phosphoglyceric
acid (PGA), a 3-carbon acid, was always the first stable product of CO_2
uptake. It is now widely recognized that some plants assimilate CO_2 via
a pathway leading to the formation of 4-carbon acids, either malate or
aspartate, as the first stable products. In the latter, CO_2 is combined

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with a 3-carbon receptor, phosphoenolpyruvate (PEP). Furthermore, there is a variation on the theme of 4-carbon acid production which allows some plants to assimilate CO_2 in the dark instead of in the light. The symbols used to designate these pathways are "C-3" for the traditional PGA plants, "C-4" for those that produce initial malate or aspartate in the light and "CAM" for those that assimilate large quantities of CO_2 at night and store it as malate until daytime (Ting et al. 1972). CAM is an acronym for Crassulacean acid metabolism, stemming from the plant family Crassulaceae in which dark CO_2 fixation was first studied in detail.

Distinctive structural characteristics are associated with these alternative pathways (Fig. 2). The leaves of C-3 plants are what might be termed typical leaves, the kind usually represented in general biology textbooks. The leaves of C-4 plants are unique in having a sheathing cylinder of bundle cells, densely packed with chloroplasts, surrounding the vascular traces of the leaf. The bundle cells appear as small green rods under the magnification of a hand lens. This anatomical feature is known widely by the German designation "Kranz". All C-4 plants have it in some form. Loosely-packed, spongy mesophyll tissue surrounds the bundle sheaths. It is in this spongy tissue where CO_2 is initially combined with PEP to form the 4-carbon acids. The resulting malate or aspartate is transported to the bundle-sheath cells where decarboxylation releases the CO_2 to the regular C-3 process.

CAM plants are those more traditionally called succulents and may have the CO_2 assimilation apparatus in the form of fleshy stems as well as or in the place of leaves. In any event, there is a considerable quantity of living cell material with reduced chlorophyll concentrations, arranged in close proximity to the peripheral tissue which contains most of the photo-synthetic pigment. Cells containing chlorophyll have large vacuoles which appear to serve as reservoirs for the malate formed during the night (Fig. 3).

Ecological significance is widely ascribed to these contrasting CO_2 assimilative processes. Important environmental relationships have been shown in experimental settings. The temperature optimum for photosynthetic rate for C-4's is usually observed to be higher than for C-3's (Fig. 4). Also, the maximum rate of photosynthesis is noticeably higher. In view of this, it is widely postulated that such plants have evolved as superior forms supposedly due to their ability to use water more efficiently in hot arid environments (Black 1971). CAM plants are also regarded as having unusually high potential for water use efficiency (Johnson 1975). Their advantage stems from two sources: 1) the opening of their stomatal pores at night while temperatures are reduced over daytime values so as to allow gaseous exchange to take place while the diffusion pressure gradient for water vapor between the plant and the air is at its daily minimum, and 2) the possession of the same highly efficient enzymatic system as C-4s for the initial capture of CO_2 molecules. In the first instance, if all else is equal, carbon dioxide uptake, which follows the same diffusion path as the transpiration stream but in the opposite direction, will not be

Figure 2. Growth habit and cross-sectional views of the photosynthetic tissue
           of three species from the California desert selected to show the
           distinctive structural features associated with the C-3, C-4 and CAM
           systems of photosynthesis. In the case of Opuntia basilaris,
           approximately one-tenth of a joint thickness is represented in the
           cross-section. (BS) bundle sheath, (C) chlorenchyma, (E) epidermis,
           (M) mesophyll, (P) parenchyma, (SC) substomatal cavity, (T) trichome
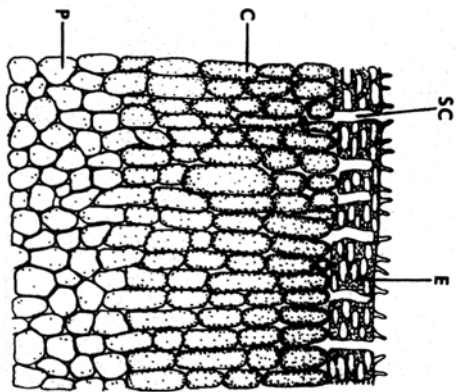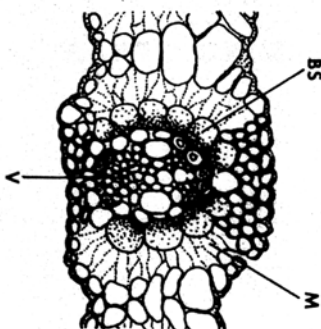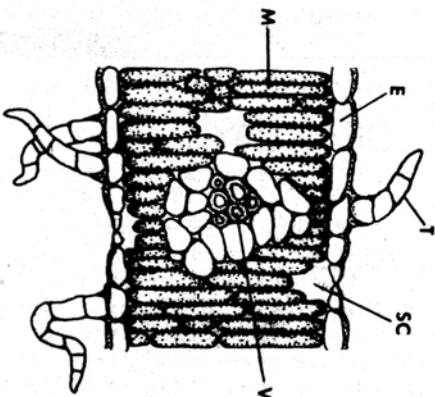   and (V) vein.

CAM

OPUNTIA BASILARIS

P C SC E

C₄

HILARIA RIGIDA

BS M

C₃

ENCELIA FARINOSA

M E T SC V
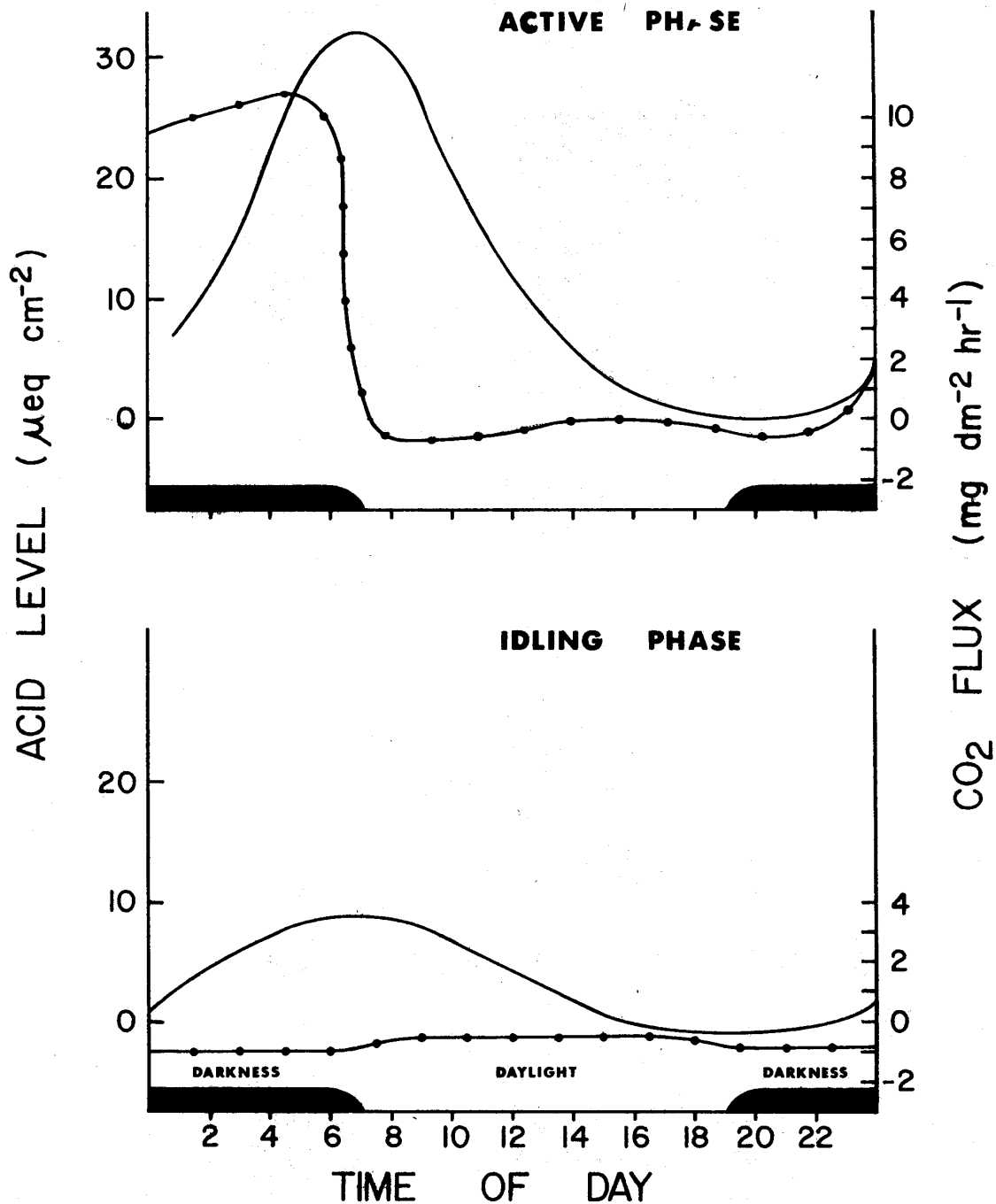
Figure 3. Generalized pattern of acid flux (————) and CO_2 exchange (•—•—•—•) in Opuntia basilaris, a typical CAM plant, under low (ACTIVE PHASE) and high (IDLING PHASE) water stress. Acidity increases by the conversion of CO_2 to organic acids. It decreases as a result of the CO_2 being released and fixed in photosynthesis. In the active phase most of the CO_2 comes from the atmosphere. In the idling phase, CO_2 comes from respiration of the plant tissue itself, thus conserving the plant's carbon supply.

Figure 4. The generalized relationship between leaf temperature and CO2 uptake for plants exhibiting the C-3, C-4 and CAM photosynthetic pathways.

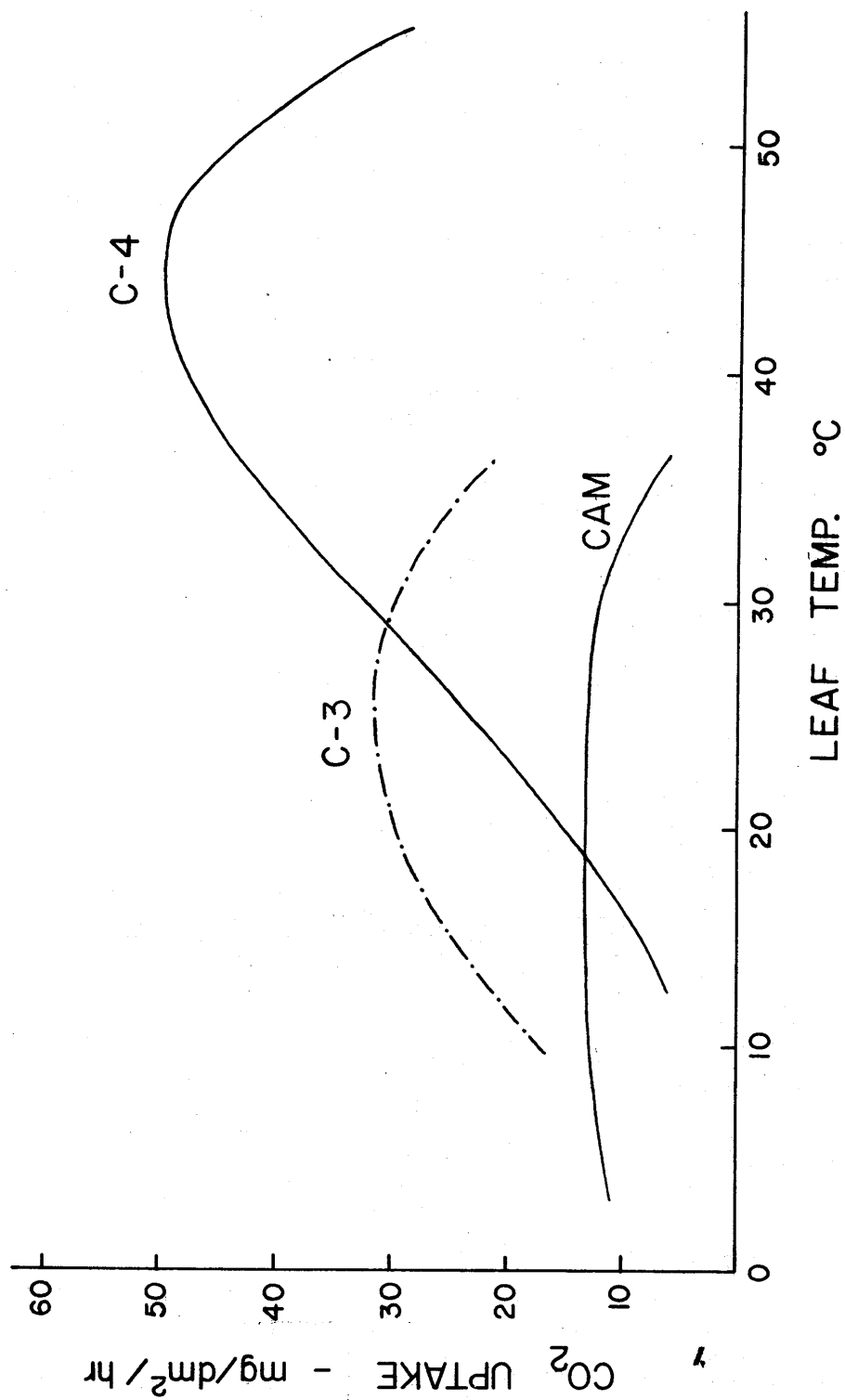greatly affected by temperature. However, the reduction in transpiration achieved by stomata opening during the cool night instead of the warm day may easily be by a factor of three.

In addition, succulent plants have the capacity to maintain moderate levels of metabolic activity by recycling their own respiratory CO_2. By this process, they maintain a physiological readiness which enables them to respond quickly to small amounts of precipitation (Fig. 3). High evaporation rates in the desert often completely dissipate meager amounts of rainfall before more sluggish species are able to "turn on" their vital processes.

The environmental relationships of these structural functional types may be considered from both the floristic and community points of view. In terms of the flora, about 85% of the 1,000 or so species of higher plants found in the California desert (cf. Munz 1974, Jaeger 1941, Johnson 1968) are C-3's; around 11% are C-4's and 4% are CAM's (Table 3). Such percentage figures must be considered as approximate at this point since many of the rarer species have not yet been appropriately characterized. The emerging pattern at the generic and familial level (Evans 1971, Tregunna et al. 1970, Krenzer et al. 1975) indicates, however, that reliable estimates are possible and may be justified for the purpose of deciphering general trends (see Appendix B and C). It is perhaps fortuitous that nearly the same proportions as noted for species having the C-4 and CAM pathways also hold at the family level, i.e., of 102 families (see Appendix A), 10 have C-4 representatives and 4 include or are wholly CAM's.

More than half of all the C-4 species belong to the grass family (Poaceae), with the same being true with respect to CAM and the Cactaceae. This is not surprising since these two families provide classic textbook examples for the processes under consideration.

Information from published floras (Munz 1974, Jaeger 1941, Twisselmann 1967) along with my own field data allows for a simple evaluation of the distribution of the most prominent species showing C-4 and CAM characteristics (Tables 4, 5 and 6). The presence or absence in the southwest Mojave of the species listed in the tables was determined from the Kern County flora prepared by Twisselmann. Kern County embraces a majority of the arrowpoint-shaped area (Fig. 1) which I have already referred to as the southwest Mojave. The apparent absence of many CAM and C-4 species in this area is rather remarkable (Table 4). In the case of CAM's, Joshua-tree (Yucca brevifolia) is the only species found in abundance (Yucca whipplei, a probable CAM, is also found in the area but is more of a coastal than a desert element). The three species of cacti indicated are found only sparingly.

Differences in CAM plants between the eastern Mojave and Colorado appear at the family level. Cacti are more common in the lower desert, particularly representatives of the genus Opuntia. Two very abundant members of the Agavaceae, Yucca brevifolia and Yucca shidigera, are characteristic of the eastern Mojave.

Table 3. Taxonomic profile of desert plant families that show or are suspected of showing either C-4 or CAM structure and function.

Family	Number of Genera	Number of Species
C-4's		
Aizoaceae	2	2
Amaranthaceae	2	4
Asteraceae	1	1
Chenopodiaceae	4	17
Cyperaceae	1	2
Euphorbiaceae	1	11
Nytaginaceae	2	6
Poaceae	23	63
Portulacaceae	1	2
Zygophyllaceae	2	4
Total	39	112
CAM's		
Agavaceae	2 (3)?	6
Aizoaceae	1	1
Cactaceae	9	29
Crassulaceae	2	4
Total	14	40

Table 4. General distribution of CAM species making important contributions to the vegetation of the California deserts. The number of + indicates relative abundance; — means absent.

| Family | Species | Distribution | | |
		Colorado	East Mojave	Southwest Mojave
Agavaceae	Agave deserti	++	—	—
	A. utahensis	—	+	--
	Yucca baccata	—	+	—
	Y. brevifolia	—	+++	++
	Y. schidigera	+	++	—
Cactaceae	Carnegiea gigantea	+	—	--
	Echinocactus polycephalus	+	+	+
	Echinocereus engelmannii	++	+	--
	E. triglochidiatus	+	+	—
	Ferocactus acanthodes	++	—	--
	Mammillaria tetrancistra	+	+	—
	Opuntia acanthocarpa	+++	+	--
	O. basilaris	++	+	+
	O. bigelovii	+++	+	--
	O. chlorotica	++	—	—
	O. echinocarpa	++	++	+
	O. erinacea	+	+	--
	O. phaeacantha	+	—	--
	O. ramosissima	++	++	—

Table 5. General distribution of vegetationally important perennial species that exhibit "Kranz anatomy" (C-4 photosynthesis) in the California deserts. Number of + indicates relative abundance; -- means absent.

Family	Species	Distribution		
		Colorado	East Mojave	Southwest Mojave
Amaranthaceae	Tidestromia oblongifolia	+	++	--
Chenopodiaceae	Atriplex canescens	+	++	+
	A. confertifolia	--	+	--
	A. hymenelytra	+	++	+
	A. lentiformis	+	+	+
	A. polycarpa	+	+	++
	A. spinifera	--	+	++
Euphorbiaceae	Euphorbia albomarginata	+	+	+
	E. polycarpa	+	+	--
Poaceae	Aristida californica	+	+	--
	A. wrightii	+	+	--
	Bouteloua curtipendula	+	+	--
	B. eriopoda	--	++	--
	B. gracilis	--	+	--
	Erioneuron pulchellum*	+	+	--
	Hilaria jamesii	--	+	--
	H. rigida	+	+	--
	Muhlenbergia porteri	+	+	--
	M. rigens	+	+	+
	Panicum urvilleanum	+	+	--
	Sporobolus airoides	+	+	+
	S. contractus	+	+	--
	S. cryptandrus	+	+	--
	S. flexuosus	+	+	--

* May also behave as an annual

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Table 6. General distribution of the most common summer annuals in the
California deserts. All listed have "Kranz anatomy" and presumably
C-4 photosynthesis. Number of + indicates relative abundance;
-- means absent.

Family	Species	Colorado	East Mojave	Southwest Mojave
Aizoaceae	Mollugo cerviana*	+	+	—
Amaranthaceae	Amaranthus fimbriatus	+	+	--
	A. palmeri	+	+	—
Asteraceae	Pectis papposa	++	++	--
Chenopodiaceae	Atriplex elegans	+	+	—
	A. rosea*	+	+	+
	Salsola iberica*	+	+	+
Euphorbiaceae	Euphorbia micromera	+	+	--
	E. setiloba	+	+	—
Nyctaginaceae	Allionia incarnata**	++	--	--
	Boerhaavia coulteri	+	+	--
	B. erecta	+	+	—
	B. triquetra	+	+	--
	B. wrightii	+	+	—
Poaceae	Aristida adscensionis	+	+	—
	Bouteloua aristidoides	+	+	--
	B. barbata	+	+	—
	Erioneuron pulchellum**	+	+	—
Portulacaceae	Portulaca mundula	—	+	—
Zygophyllaceae	Kallstroemia californica	—	+	--
	K. parvifolia	—	+	—
	Tribulus terrestris*	+	+	+

* Introduced species

** Sometimes a short-lived perennial

Species of C-4 plants also show marked reductions in the southwest Mojave (Tables 5 and 6). This reduction cannot be ascribed merely to the smaller size of the area represented since this southwest section is certainly large enough to provide the topographic variety found in other parts of the desert. The growth habit of the C-4 plants, i.e., whether they are shrubs, perennial herbs or annual herbs, helps to further discern a pattern that may be related to environmental responses. Most C-4's are herbs. Woody plants which exhibit this C-4 feature appear to have been derived from herbaceous ancestors (Stebbins 1972). Species of Atriplex provide prime examples of the few known woody representatives (Table 5). It is the woody representatives that are most common in the southwestern part of the desert. Herbaceous C-4's, both perennials and annuals, occur there only in specialized habitats. In the case of the summer annuals, none of the natives from Table 6 are even listed in Twisselmann's flora of Kern County (1967). The three introduced species which do occur occupy for the most part habitats with a high degree of surface disturbance.

Differences in the climatic regimes among the sections of the California deserts that were noted earlier (Table 1) are likely correlated in a causative way to these distribution patterns. The lack of summer precipitation in the southwest Mojave must certainly serve as a limitation to summer annuals. Even in the eastern Mojave and the Colorado, where the chance of summer rain is greatly increased, specific localities may go years without summer moisture. The native summer annuals appear to be completely dependent on summer thunder showers. Their capacity to function efficiently in photosynthesis at high temperatures is a must if they are to complete their life cycle before the evaporation of moisture received as summer showers. I would suggest that summer moisture is an important factor in determining the distribution of CAM as well as C-4 plants. It seems probable that the winter moisture supply may extend well into the summer in the case of Atriplex shrubs growing on deep soil in the west Central Valley and southwestern Mojave.

It should be noted that a few herbaceous C-3 species grow throughout the desert in the summer time. Among the most common are Asclepias erosa, Coldenia plicata, Cucurbita palmata, Datura meteloides, Mirabilis froebelii, Palafoxia linearis, Psathyrotes ramosissima and several genera in the Capparaceae. Their success suggests perhaps an intermediate, or even another type, of gas exchange strategy.

Moving now to a consideration of just how important the three photosynthetic types are in the vegetation of the desert, as opposed to its flora, it becomes readily apparent that the collective plant material for a given area can be referred to one of seven possible photosynthetic categories. That is, the vegetation may be 1) all C-3; 2) all C-4; 3) all CAM; 4) a C-3/C-4 mixture; 5) a C-3/CAM mixture; 6) a C-4/CAM mixture, or 7) a C-3/ C-4/CAM combination.

In theory, it should be possible to classify all vegetation of the desert according to this scheme without reference to formally defined taxonomic units. It is impractical to do so at this point, however, since species

designations provide the most convenient handle for making detailed consider-
ations. I realize that this is contradictory to my earlier argument showing
that a given taxon, even at the species level, may represent an array of
structural and functional types. Nevertheless, characterization of the
photosynthetic systems by species is believed to provide sufficient refine-
ment for the purpose at hand. The most convenient approach for establishing
the relative importance of the three photosynthetic types in the vegetation
of the entire desert is to relate them to the plant communities defined by
species composition that have already been considered (Table 2). A combina-
tion of the classification systems of Knapp and Thorne along with the addi-
tions suggested above are employed for that purpose as set forth below in the
seven possible photosynthetic categories.

1. C-3. Communities that are comprised essentially of C-3 species
alone are:

Sagebrush scrub   Desert riparian woodland
Blackbush scrub   Desert microphyll woodland
Pinyon-juniper woodland   Desert oasis woodland
Creosote bush scrub   Winter annuals
Hopsage scrub

Not only does the above listing represent the majority of the community
types but it also includes those which cover the most extensive areas of
the desert. The creosote bush scrub in California is judged to occupy more
area than all of the other types combined. Three communities, sagebrush
scrub, blackbush scrub and pinyon-juniper are best developed outside of
California. The woodlands are small and localized with respect to supple-
mental ground water. Their importance from the standpoint of productivity
is far greater than the small area which they occupy would indicate. Winter
annuals as a community have a temporal identity rather than a spatial one.
They occur throughout the desert but not every year at each locality. Their
special role in contrast to summer annuals will be considered further below.

2. C-4. Communities that are comprised chiefly of C-4 species are:

Shadscale scrub
Allscale scrub
Desert holly scrub
Saltgrass meadow
Summer annuals

The first three above are characterized by species of the genus _Atriplex_,
or saltbush. The common name accurately reflects a tendency for these plants
to be associated with saline habitats. Shadscale scrub appears primarily in
alkali sinks in the Mojave although this is not necessarily the case in the
Great Basin where it ranks as one of the major vegetation types. The allscale
scrub and desert holly scrub are likewise not so restricted in the southwest-
ern California desert region but seem to favor deep soils with high water
storage capacities. Saltgrass meadows, dominated by _Distichlis spicata_, are

restricted to moist salty habitats. Summer annuals are not found in the western Mojave or Death Valley. Throughout the rest of the desert they occur spottedly during the late summer and early fall whereever summer thundershower activity provides enough moisture to stimulate their growth. The characteristic pattern is one of extreme patchiness. Islands of annuals are produced every year somewhere in the desert. The size and location of these islands are strictly functions of the summer thunderstorm activity.

3. CAM. Communities that are comprised chiefly of CAM species are:

Stem-succulent scrub
Semi-succulent scrub (in part)
Joshuatree woodland (in part)

Pure stands of CAM species seldom occur except in very local conditions. Opuntia bigelovii often forms dense patches covering many acres, e.g., the Sacramento Mountains near Needles. Dense Joshuatree stands, with other species of Yucca and Opuntia as co-dominants, occur locally at mid-elevations in the New York Mountains. Agave deserti, Yucca schidigera, Ferocactus acanthodes, Opuntia acanthocarpa, Opuntia basilaris and Opuntia bigelovii make up the bulk of the vegetation at the 3,000' level in the Deep Canyon Desert Research Preserve near Palm Springs.

4. C-3/C-4. The Mojave riparian scrub, which occurs in narrow ribbons along the drainage channels throughout the higher desert has C-3's such as Hymenoclea salsola and Acacia greggii and C-4's such as Atriplex polycarpa and A. canescens as common representatives.

5. C-3/CAM. Much of the area commonly designated as Joshuatree woodland in the southwestern Mojave has an understory of C-3 shrubs. Asteraceous species belonging to genera such as Chrysothamnus, Haplopappus and Acampto-pappus are important. Also extensive areas commonly designated as creosote bush scrub have sizeable representations of Opuntia spp. and could properly be considered as belonging here.

6. C-4/CAM. This combination is rare but east of the New York Mountains perennial C-4 grasses belonging to the genera Hilaria and Bouteloua grow in abundance among scattered Joshuatrees. Together they dominate the major portions of several valleys.

7. C-3/C-4/CAM. Rich assemblages of plants representing all three photosynthetic types occur at elevations between 1,200 m. (4,000') and 1,800 m (6,000') in the foothills of scattered mountain ranges throughout the Mojave. These areas with a Joshuatree aspect harbor other CAM species of both Yucca and Opuntia. The C-4 Hilaria rigida is commonly abundant and C-3 shrubs belonging to the genus Lycium and Prunus are frequent. This type of mixture is rather common wherever CAM species are prominent.

Annuals. The temporal communities composed of summer annuals and winter annuals have been referred to several times above and merit further consider-ation. Even though deserts are frequently characterized as therophytic en-vironments, a la Raunkier (Mueller-Dembois & Ellenberg 1974), the position

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which annuals occupy in desert vegetation is still not well understood. Most life form compilations for deserts show annuals as representing about 40% of the total flora. This is also true in California if the whole broad geographic region termed "desert" is considered. If, however, smaller segments of the desert are analyzed then the probable significance of annuals looms even larger. In scaling down from the whole desert to increasingly more specific habitats, a dramatic increase occurs in the proportion of annuals in the flora (Table 7). The increase occurs as the communities of "non-desert habitats", embraced under the broad geographic designations, are eliminated, e.g., the white fir forest of Clark Mountain. In typical desert environments, biomass production of annuals in good years may be equal to that for perennials (Norton 1974).

Observations made in the Lucerne Valley (Mojave Desert) during the period between 1971 and 1974 provide additional insight on the environmental relationships of annuals (Johnson, et al., a. In preparation). Summer moisture stimulated the growth of summer annuals on both a rocky and a sandy bajada which were under investigation during the summer of 1972. Annuals on the rocky bajada were stimulated by moisture supplied by sprinkler irrigation. Annuals on the sandy bajada, however, were not stimulated by sprinkler irrigation but an intense thundershower later in the summer (August) caused a profusion of annual growth generally all along the storm's path which included the irrigation plot. All the annual species that grew in response to summer moisture had C-4 anatomy. The most abundant were Pectis papposa and Euphorbia setiloba. Fifteen of the 22 species listed in Table 6 were found on or in the vicinity of the study plots. It appears that essentially the same combination of summer annuals shows up in the California deserts wherever sufficient summer moisture occurs. Minor species, such as those of Kallstroemia and the native Portulaca, are restricted to the more easterly parts of the state. As a community then, summer annuals have a wide geographic distribution but exhibit only a short temporal though re-occurring existence.

The germination and development of winter annuals also depends on the availability of moisture during the appropriate season (Beatley 1974b). None have been observed to grow in response to rain in the summer. Their growth cycle is triggered only by fall and winter precipitation which is usually distributed more uniformly in both time and space than that which falls during the summer. As a result, winter annuals often exhibit a continuous distribution over vast areas of the desert. Such a pattern is in contrast to the patchiness of their summer counterparts. The pattern of consistent fall-winter precipitation is especially pronounced in the southwestern Mojave and southwest Central Valley. In the eastern Mojave and Colorado deserts, the failure of sufficient fall-winter precipitation for the development of annuals is more common and specific localities may have virtually no annual growth for several years at a time.

In the fall and winter of 1972-1973, precipitation was exceptionally heavy and uniform throughout the entire region of the California deserts. The growth of annuals was spectacular. Detailed studies of the Lucerne Valley study areas embraced this period. Observation on winter annuals provided contrasts to those on summer annuals in several respects. The numbers

Table 7. Contribution of annuals to plant species richness in geo-
graphical units of varying size.

Geographical Unit	Number of Species	% Annuals	Reference
California Deserts	764	43	Jaeger (1941)
Deep Canyon Drainage	334	47	Floristic list for Deep Canyon watershed (1973).
Johnson Valley	87	60	Vasek et al., (1974) Plant list from combined study plots & transects.
Rocky Slope (Lucerne Valley)	28	82	Johnson et al. (a. In preparation)
Bajada (Lucerne Valley)	25	88	Johnson et al. (a. In preparation

of species of winter annuals was much greater. This increase in species richness appears to be accompanied by more specific habitat associations. For example, the display of winter annuals on the rocky and sandy bajadas considered above with respect to summer annuals was very different even though the perennial cover was essentially the same on both. It is apparent that the species composition of winter annual communities changes markedly with type of substrate. The similarity coefficient for the rocky and sandy bajadas, using the Jacard index, was .86 on the basis of perennial cover but only .06 on the basis of winter annual density. The maximum value for the index is 1.0. When annuals and perennials were compared separately for a number of sites having different substrates it was found that annuals were most sensitive to changes in substrate type and that the most similar substrates yielded the highest similarity values for annuals (Johnson, et al., a. In preparation). Whether this observation is merely fortuitous or represents a finely tuned higher evolutionary unit remains to be established.

During most years, the temporal distinction between summer and winter communities is nearly complete. Occasionally, however, overlap in late summer and early fall rains causes a blurring of this distinction in that winter annuals may have begun growth before the summer annuals have completed their cycle.

The case for recognizing summer and winter annuals as community types in their own right is made primarily on the basis of their great dependence on the temperature and moisture features of the physical environment. At some points, however, they do appear to interact with each other and also with the perennial species among which they grow. Winter annuals growing during the 1972-1973 season were observed to be negatively affected by the summer irrigation and thundershowers of the preceding summer. A visible reduction in the density and vigor of winter annuals on the irrigated plots over the immediate surroundings was substantiated quantitatively (Table 8). The reduction in winter annuals was particularly marked in the areas between the shrubs where summer annuals had grown most abundantly. The reason for the negative response is not understood but biotic interactions appear to be a more likely source for explanation than purely physical considerations.

It is a common observation that some species of annuals often exhibit positive associations with shrubs. This relationship is more obvious on sandy bajadas than on rocky slopes and it was further intensified by irrigation on the study plots. The association is undoubtedly related, at least in part, to the effect that shrubs may have on the soil water supply. A water-repellant crust often forms near the soil surface under shrubs growing on light-textured soils (Adams, et al. 1970). In the case of creosote bush on the sandy bajada, such a crust causes the water falling through the bush to drain toward the outer periphery of the crown where it is concentrated and sinks down into the soil. Because of this concentrating effect, moisture penetrates deeper into the soil and becomes less susceptible to surface evaporation than would be the case if it were uniformly distributed. The ultimate consequence of this is that more water is made available for

Table 8. Density of winter annuals (individuals/meter) in the Spring of 1973
on the irrigation plots and adjoining areas (Johnson et al., a. In
preparation).

	ROCKY SLOPE		SANDY BAJADA		
	(a)	(b)	(c)	(d)	(e)
	Irrigation 1972	No Irrigation 1972	Irrigation plus Summer rain 1972	Summer rain 1972	No Summer rain 1972
Eriastrum eremicum	—	0.13	2.55	3.55	0.79
Erodium cicutarium	0.01	0.64	9.90	15.84	46.19
Eschscholzia parishii	10.52	25.39	0.41	1.09	0.10
Gilia latiflora	9.90	12.78	—	—	—
Gilia scopulorum	—	—	6.02	11.26	6.06
Phacelia fremontii	—	—	9.95	6.04	1.75
Schismus barbatus	0.31	0.07	7.96	9.27	4.07
Others	3.02	4.17	3.37	5.10	6.29
TOTAL	23.85	42.18	39.80	52.14	75.26

	(a)	(b)	(c)	(d)	(e)
Number of 0.1 sq. meter plots sampled	96	455	98	341	202
% of plots without plants	16.7	8.6	15.3	6.7	0.7
No. of species observed	11	19	12	21	19
Species/plot	0.115	0.042	0.122	0.062	0.063

plant growth (Johnson et al. 1975). Annual plants tend to be concentrated in the zone where the water is collected (Johnson, et al., b. In preparation). This interpretation is an extension of that provided by Adams, et al. (1970) who imply that annual growth is reduced because of water repellancy under shrubs. The question may be asked here also as to whether this relationship is merely fortuitous or an expression of a highly integrated evolutionary unit. If the latter is the case, then perhaps the winter and summer annuals should be considered at the rank of ecological groups (Mueller-Dombois and Ellenberg 1974) contributing to a more complex community.

SUMMARY AND CONCLUSIONS

The Southern California deserts can be conveniently divided into three separate units: the Mojave, the Colorado and the Southwest Central Valley, on the basis of physiography, climate and plant life. The boundaries between the Mojave and Colorado, though distinct on the western interface, become blurred toward the east.

Important insights on the plant life of the deserts can be gained from a combination of the floristic, community and vegetation points of view. Floristic differences in the deserts are pronounced. The tendency toward endemism is greatest in the Mojave where evolutionary centers such as Death Valley and the southwestern corner show high incidences of neoendemics. Numerous taxa, important in the Sonoran Desert, reach their northern limit at the Mojave-Colorado interface.

A variety of plant communities have been recognized as having differentiated from these divergent floras. Classification schemes that have been devised by various botanists represent, to a large extent, the different purposes of the investigators. The number of units recognized varies from six for Munz and Keck to 17 for Thorne. Community descriptions are in large part subjective. Quantitative work should be done to establish the validity of the types recognized. Plant communities defined on a floristic basis should not necessarily be expected to form discrete functional units in the desert environment.

Desert vegetation has a number of distinct structural features, such as small leaves and green stems. The functional relationships of such features are most generally poorly understood. A point of refinement in this direction now appears possible with respect to the alternative photosynthetic pathways, C-3, C-4 and CAM, and their associated structural peculiarities. The C-3 system is the most common and evidently the most successful from the floristic, community and vegetation cover-biomass points of view. Species with the C-4 system do not appear to be taking over the desert as should be in the case according to implications in the current literature attesting to the "superiority" of this system in hot-arid environments. Instead, C-4's appear to fit into rather narrow environmental niches in the desert, defined by moisture availability during periods of high temperatures and/or saline habitats. CAM plants are not abundant in the driest part of the desert either, but reach their greatest development in areas where summer

rains are most probable. The contribution of CAM plants to the vegetation biomass as a whole is large, however, in proportion to the number of species that exhibit the system. Their capacity to conserve carbon by recycling their own respiratory CO_2 is thought to contribute significantly to their success. It might be suggested that a modification of this carbon conservation theme be of greater importance to the survival of green-stem shrubs than the more commonly held view that green stems act as some sort of superior substitute for leaves.

Desert annuals represent two types of opportunists that appear to function quite independently. The summer annuals are all C-4's and the winter annuals are all C-3's. The winter annuals appear to be more finely integrated into the desert environment than the C-4's.

The classification of vegetation based on photosynthetic types must be considered preliminary at this point. It is presented as an example of how functional criteria may be employed for gaining a greater understanding of the ways plants are integrated into the desert environment. The consistent correlation that exists between leaf structure and photosynthetic type cuts across large taxonomic boundaries and suggests that a high degree of convergence has taken place in the evolution of both biochemical processes and gross anatomy. As such phenomena become better known they should take their place as important considerations in the erection of phylogenetic schemes in taxonomy as well as in their recognition and definition of functional units of plant assemblages in the landscape.

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Appendix A.   Plant families represented in the deserts of Southern
California.

Acanthaceae	Fabaceae	Potamogetonaceae
Agavaceae	Fagaceae	Primulaceae
Aizoaceae	Fouquieriaceae	Pteridaceae
Amaranthaceae	Frankeniaceae	Rafflesiaceae
Amaryllidaceae	Garryaceae	Ranunculaceae
Anacardiaceae	Gentianaceae	Resedaceae
Apiaceae	Geraniaceae	Rhamnaceae
Apocynaceae	Hydrophyllaceae	Rosaceae
Arecaceae	Iridaceae	Rubiaceae
Asclepiadaceae	Isoetaceae	Ruppiaceae
Asteraceae	Juncaceae	Rutaceae
Berberidaceae	Krameriaceae	Salicaceae
Betulaceae	Lamiaceae	Santalaceae
Bignoniaceae	Lemnaceae	Saururaceae
Boraginaceae	Lennoaceae	Saxifragaceae
Brassicaceae	Liliaceae	Scrophulariaceae
Burseraceae	Linaceaee	Selaginellaceae
Buxaceae	Loasaceae	Simarubaceae
Cactaceae	Loranthaceae	Solanaceae
Callitrichaceae	Malvaceae	Sterculiaceae
Campanulaceae	Martyniaceae	Tamaricaceae
Capparaceae	Najadaceae	Typhaceae
Caprifoliaceae	Nyctaginaceae	Ulmaceae
Caryophyllaceae	Oleaceae	Urticaceae
Celastraceae	Onagraceae	Verbenaceae
Ceratophyllaceae	Orchidaceae	Vitaceae
Chenopodiaceae	Orobanchaceae	Zannichelliaceae
Convolvulaceae	Papaveraceae	Zygophyllaceae
Crassulaceae	Pinaceae	
Crossosomataceae	Plantaginaceae	
Cucurbitaceae	Poaceae	
Cupressaceae	Polemoniaceae	
Cuscutaceae	Polygalaceae	
Cyperaceae	Polygonaceae	
Elaeagnaceae	Polypodiaceae	
Ephedraceae	Portulacaceae	
Equisetaceae		
Ericaceae		
Euphorbiaceae		

Appendix B. Genera containing or suspected of containing C-4 species reported as occurring in the deserts of Southern California.

Allionia
Amaranthus
Aristida
Atriplex
Boerhaavia
Bouteloua
Chloris*
Cynodon*
Cyperus
Dactyloctenium*
Digitaria*
Distichlis
Echinocloa*
Elusine*
Eragrostis*
Eriochloa*
Erioneuron
Euphorbia

Halogeton*
Hesperochloa
Hilaria
Kallstroemia
Kochia
Leptochloa
Mollugo
Mulenbergia
Panicum
Paspalum*
Portulaca
Salsola*
Setaria*
Sorghum*
Spartina
Sporobolus
Tidestromia
Trianthema
Tridens

*Introduced

Appendix C. Genera containing or suspected of containing CAM species reported as occurring in the deserts of Southern California.

Agave
Carnegiea
Coryphantha
Dudleya
Echinocactus
Echinocereus
Mammillaria
Neolloydia
Opuntia
Sesuvium
Yucca